

Never lose your sense of wonder: reflections of a stream biologist

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Early days

Auckland University

During a field trip to Piha in the Waitakere Ranges west of Auckland I came across an adult stonefly beside a track. When I asked what its name was no one knew. I checked it out in Tillyard's paper⁷⁸, the standard reference at the time, and discovered it was *Nesoperla trivacuata* (now placed in *Acroperla*). This was the start of my research career. Subsequently, I described the larva of this stonefly and examined its life history in Swanson Stream as part of my Masters research. Like several other New Zealand gripopterygids its larvae show tendencies towards terrestriality that I documented in an early paper from the thesis⁸⁷.

The zoology courses taught at Auckland in the early 1960s gave us a strong grounding in the structure, diversity and relationships of animals and were based on classic textbooks such as Grove and Newell³⁷, and "BEPS" (Borradaile, Eastham, Potts & Saunders)⁹. There were no courses devoted to ecology or physiology and only rudimentary cell biology. Marine biology took off at Auckland following the appointment of John Morton to the chair in 1960 and Jim Pendergrast and Don

Cowley taught aquatic entomology and freshwater biology. Their excellent little book "An Introduction to New Zealand Freshwater Insects"⁶⁴ was written while I was a student of theirs and while Don was doing his PhD on the taxonomy of caddisflies²⁰. Don and I did a lot of fieldwork together in places like the Waitakere and Hunua Ranges, and I consider him to be an influential mentor. My first two scientific papers were in the Auckland University Field Club journal *Tane* and were a report on the stream fauna of Little Barrier Island streams⁸⁶, and prophetically, a key to the larvae of stream insects⁸⁵. I suspect that my subsequent "Guide to the Aquatic Insects of New Zealand" (now in its 4th edition)¹⁰⁴, which had its birth in that early key, has been my most useful (and certainly most practical) contribution to aquatic biology and its study in New Zealand.

John McLean, who helped sample the streams on Little Barrier, was my other regular fieldwork companion at Auckland. His Masters thesis was on the life history of the mayfly *Oniscigaster*, whose fast-swimming nymphs were collected with a specially designed net⁵⁷. John also published observations on the egg-laying flights of several mayfly species⁵⁸ and

remains one of the few people to have done so in this country. Later he worked at the University of the South Pacific in Fiji and is now a distinguished forest entomologist at the University of British Columbia in Canada.

Maureen Barclay (now Lewis) was the only other student doing freshwater research in my year at Auckland. She worked on micro-crustaceans and pond biology³ and had the infinite patience needed to dissect the legs from minute ostracods and copepods. She later completed a PhD on the systematics and zoogeography of harpacticoid copepod^{47,48}. The book she wrote with Ann Chapman "An Introduction to the Freshwater Crustacea of New Zealand"¹⁴ represented a publishing milestone in New Zealand limnology and its fully revised successor is awaited with anticipation.

Massey University

I went to Massey as a junior lecturer at the start of 1966. Junior lecturers could enrol part-time in a PhD, which is what I did, along with teaching entomology to horticulture students and running zoology labs. My thesis problem was to sort out the systematics of the freshwater gastropod genus *Potamopyrgus* (Figure 1) and to investigate some other aspects of its biology. This proved to be an ideal topic to pursue part-time as the collecting and microscope work could be done in bursts as time and teaching commitments allowed. My biggest break was provided by Dick Dell, then director of the Dominion Museum, who gave me his entire collection of reprints on *Potamopyrgus* and other freshwater hydrobiids. His revisions of the molluscan genera *Hyridella*, *Physastra*, *Lymnaea* and *Myxas*, and discussions with a somewhat skeptical Winston Ponder who wasn't too

sure that an entomologist could work on molluscs, gave me the idea to study *Potamopyrgus* in the first place. Winston had been a student contemporary at Auckland and is well known in malacological circles for his exhaustive studies on micro-molluscs including Hydrobiidae.

My research at Massey was supervised by Wallie Clark, Lou Gurr and Tim Brown and resulted in the lumping of all the described freshwater species and subspecies of *Potamopyrgus* into a single species *P. antipodarum*⁸⁸. *Potamopyrgus pupoides*, which inhabits brackish-water was retained and I described a new species *P. estuarinus*. The latter can be incredibly abundant on estuarine mudflats that are exposed at low tide and had been overlooked because its shell resembles that of some *P. antipodarum*. However, whereas *P. antipodarum* is ovoviviparous, *P. estuarinus* is oviparous. More recently, numerous new species of *Potamopyrgus* and related genera have been described from groundwaters and springs, habitats that I did not collect in. *Potamopyrgus antipodarum* has also invaded freshwaters in various parts of the world, and its potentially deleterious effect on freshwater communities in North America where it has established some large populations is currently a concern to environmental

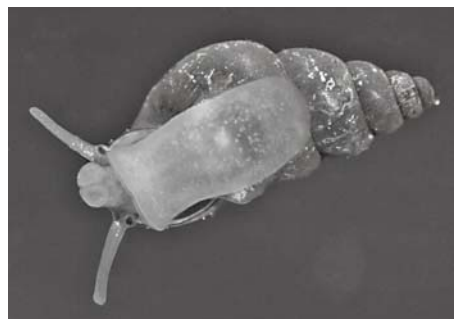


Figure 1. The gastropod *Potamopyrgus antipodarum*. Photo Angus McIntosh.

managers.

At Massey I also described the first freshwater nereid worm from New Zealand⁹⁰ and developed an interest in thermal spring faunas upon noticing fish and insects in the warm Waipahihi Stream at Taupo. Very little was known about our thermal biota at the time, despite the accessibility of many warm springs, streams and lakes. Subsequently, my wife Christine and I made a number of trips to the volcanic plateau, collecting invertebrates and algae and recording the water temperature where they were found⁸⁹. My first paper on hot spring fauna, written with Tim Brown who examined the protozoa, was published in the first issue of the *New Zealand Journal of Marine and Freshwater Research*⁹⁷.

Canada

Christine and I completed our doctorates at Massey towards the end of 1968 and took up post-doctoral fellowships at the University of British Columbia (UBC). On the way we attended the Mexico City Olympic Games where Bob Beamon broke the world long jump record. We were in the stadium at the time but as luck would have it I was looking at the shot put competition and missed it! I also missed the initial scientific meeting of the NZ Limnological Society in 1968 because my PhD oral was scheduled for the same day.

The UBC post-doc was one of the best opportunities that came my way. I was recruited by Ian Efford to work in the Marion Lake project, one of Canada's



Figure 2. Mike Winterbourn with Canterbury colleagues at the Glenariffe salmon trap 1972. From left, Vida Stout, MJW, Colin McLay and Trevor Crosby.

contributions to the International Biological Programme. This was my first opportunity to work as part of a team in which everyone's research was of at least some direct interest to the others. I worked on the life histories, energetics and trophic relations of trichopteran larvae^{91,92}, my first experience with this order of insects. At its peak over 30 students, staff, post-docs and research assistants were working at the lake. The study of energy flow was seen as a key to understanding ecosystems at the time, but although the development of a robust predictive model proved elusive⁸³, many of the individual studies undertaken on the lake were outstanding examples of innovative ecology.

I also met Colin McLay (Figure 2) for the first time at UBC where he was doing his doctoral research on ostracod ecology. I knew of him in New Zealand where he had looked at the newly discovered phenomenon of invertebrate drift as an undergraduate at Otago University⁵⁵. He wrote his significant, pioneering paper on distances drifted by stream invertebrates at UBC and I commented on a draft for him⁵⁶. Colin and I were both appointed to lectureships at Canterbury shortly afterwards and we both headed the Department of Zoology in later years.

The experience of investigating energy flow, secondary production and trophic

relationships of aquatic invertebrates (including my first gut analyses and use of ^{14}C) influenced much of my subsequently research and that of my research students at Canterbury. Some of my earliest projects there were a study of trophic relationships and production of the stonefly *Stenoperla* (Figure 3) and the mayfly *Deleatidium*⁹⁴ (Figure 4), and an investigation of the foods of free-living caddisflies⁹⁵.

University of Canterbury

From late-1970 to 2000 I was a member of the staff of the Zoology Department at the University of Canterbury. This was an exciting period for stream ecology and the publication of two important papers by Ken Cummins^{24,25} had a significant influence on the direction of my work. In the remainder of this article I pick out various research highlights and achievements of students and others with whom I was associated. These are not all encompassing, and I apologise if you do not feature. This is not a reflection on your contributions as a student or colleague I assure you.

Trevor Crosby (Figure 2) was my first PhD student, although he had started his research under Euan Young who left the university for Samoa shortly before I arrived. Trevor made a detailed study



Figure 3. An adult of the eustheniid stonefly *Stenoperla prasina*. Drawing by Karen Mason.



Figure 4. Larvae of the ubiquitous mayfly *Deleatidium*. Photo Phil Pointing.



Figure 5. From left to right, the electrofishing team of Jon Harding, Alastair Suren, Paddy Ryan and Mark Sanders at Jones Creek, near Granity in 1991.

of the blackfly *Austrosimulium tillyardianum*²¹ that included an innovative investigation of the rate with which it colonised a new channel excavated alongside Wainui Stream on Banks Peninsula. Trevor also kept detailed records of the many (often obscure) papers he had requested through the library interloan system and used them as the basis of a paper that evaluated the effectiveness of the system²². Trevor was one of the first Canterbury students to make use of computers for data analysis. Subsequently, he edited and formatted all four editions of my Guide to Aquatic Insects of New Zealand as well as contributing the section on Simuliidae²³. Kate Gregson who drew the figures for the first edition of the Guide was a second year Zoology student at Canterbury and Craig Dolphin who contributed more figures to the third edition was a Masters student in Marine Biology at the time.

Although addressing a diversity of

subjects much of my research on streams and that of my students was concerned with the structure and functioning of forest stream ecosystems and the effects of various land use practices on stream communities.

Pollution, forestry and acidification effects on streams

One of the first tasks given me by Professor Knox on arrival at Canterbury in late 1970 was to survey streams in the lower Waimakariri catchment and determine their pollution status. This work revisited the classic pollution assessment study of Hirsch⁴² and demonstrated the continuing poor water and habitat quality of the South Branch and the Kaiapoi River system. I vividly recall the way the lower Cam changed colour from red to green depending on the dyes being discharged from the woollen mill as Chris Fowles took water samples. In following years we monitored the improvement in health of the Kaiapoi River following installation by

local engineer John Cranko of an innovative filtration plant to treat fellmongery waste until the factory burnt down in 1977 and was not rebuilt^{79,108}. John Marshall also evaluated the biological condition of the Leeston Drain⁶² and demonstrated the negative effects that fine organic particles had when they filled the interstices between gravel particles within the streambed. He argued that following the annual removal of macrophytes they be removed from the immediate environs of the stream to minimise the reintroduction of nutrients from decomposing plant matter⁶¹, although whether that is done consistently is a moot point. The effect of sedimentation on streams was subsequently the subject of an excellent review paper⁷⁰ by Paddy Ryan (Figure 5) who was living on the West Coast where alluvial gold mining was having an obvious effect on stream fauna.

Investigating the effects of land use on stream fauna is a subject that appeals to many students because of its potential application and the chance that their research will make a difference. These are some examples. Jon Harding (Figure 5) found that land use had a strong effect on stream fauna in the Hanmer district with streams in pasture showing greater differences than those in native and exotic forest⁴⁰. Darren Cottam found relatively uniform invertebrate faunas in Christchurch urban streams and showed that the presence of wood aided retention of leaves and enhanced habitat for invertebrates¹⁸. Michele Widdowson also demonstrated that stream health declined below Canterbury towns despite being in predominantly rural catchments⁸⁴, and AslanWright-Stow used an extensive invertebrate data set collected for the Canterbury Regional Council to evaluate

the health of streams throughout the province¹¹⁰.

Our research on forest streams and the effects of forestry on stream communities was facilitated by grants from the Forest Research Institute and in particular the support of Colin O'Loughlin. One aspect of this work was a long-term ecological study of streams in the Maimai Experimental Area near Reefton with emphasis on community stability, the effects of buffer strips on stream fauna, and the feeding relationships of insect larvae⁹⁶. However, much of our research addressed basic questions in forest stream ecology and would have been much more difficult without Colin's open-minded attitude, for which we owe much.

Robin McCammon was my first student to work on stream ecosystem processes. He constructed an organic energy budget for Middle Bush Stream at Cass, inspired by the Fisher and Likens³³ paper on Bear Brook, and although the study dragged on for seven years his was an impressive thesis⁵¹ with strong intellectual content. The source of the very fine particles that are found in insect guts was another topic he pursued and he successfully formed particles from DOM as had been conjectured in the literature. At the same time Sally Davis and I examined breakdown of beech leaves

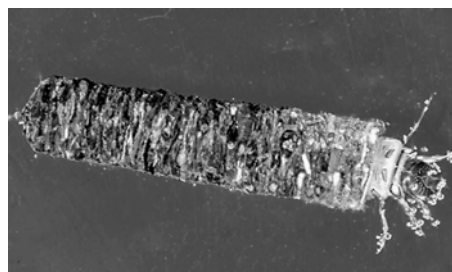


Figure 6. The final instar larva of the oeconesid caddisfly *Zelandopsycha ingens*. Photo Terry Williams.

in Middle Bush Stream and undertook the first studies of the leaf- and wood-shredding caddisfly *Zelandopsychengens*^{28,102} (Figure 6). This large, iconic species (at least to an aquatic entomologist) has been the subject of more recent studies by Angus McIntosh and his students who have found, amongst other things that the nature of its case is influenced by the presence or absence of trout⁵⁴. Leaf litter processing and the life histories of shredders were also examined by Wayne Linklater in three streams receiving different species of tree leaves on Banks Peninsula⁴⁹. Despite the trees having different leaf-fall patterns, insect life cycles in the three streams did not differ as predicted by contemporary theory²⁶. Robin McCammon's work in particular, set the stage for the groundbreaking and often innovative research undertaken by Brent Cowie and Jim Rounick.

Brent Cowie's research on Devils

Creek resulted in detailed knowledge of stream communities along the river, an understanding of the life histories of many species, especially stoneflies, and an appreciation of their trophic relationships obtained by gut content analysis¹⁹. Brent also introduced the term "browser" to describe aquatic invertebrates that inhabited stones and ingested predominantly fine detritus but also algae. His research suggested that the shredder pathway whereby fine particles ingested by collectors are produced by the feeding activity of shredders was unimportant in his streams and focused attention on stone surface organic layers. This theme was developed further by Jim Rounick.

Jim Rounick (Figure 7) did the most significant work of any of my graduate students. He came to Canterbury from Oregon State University where he had undertaken a project in their influential stream team and was interested in the "big picture" when it came to stream ecology.



Figure 7. Jim Rounick at the cutting edge. Cass spring, 1980.

I was more interested in smaller-scale processes involving invertebrates so we offered each other complementary approaches to how stream ecosystems functioned. Jim's fine work on organic layers⁶⁶ built on the earlier study by Brent Cowie, which had shown that although the chlorophyll concentration on stream bed stones differed substantially seasonally, total organic carbon concentration stayed very much the same⁹⁶. This led us to propose that non-algal components of epilithon might play a major role in supporting populations of stone-dwelling invertebrates in the absence of shredders. Jim's work that incorporated a range of approaches supported this idea. He was also the first person to use stable carbon isotopes to examine trophic relations in streams and in his initial study demonstrated differences in the isotope signatures of invertebrates in forested and grassland streams that suggested primarily allochthonous and autochthonous carbon

dependence, respectively⁶⁷. Jim made most of the carbon analyses himself at the Institute of Nuclear Sciences where he had the run of the lab in the evenings "after work". Subsequently, stable isotopes have been used with enthusiasm in many ecological studies but with varying degrees of success, as they require the right situation and assumptions to "work", convincingly.

Jim and Brent were instrumental in developing ideas that were incorporated in our paper "Are New Zealand stream ecosystems really different?"¹⁰⁷, which questioned some of the tenets of the River Continuum Concept as they applied to this country. This paper gave us, New Zealand stream ecology and the *New Zealand Journal of Marine and Freshwater Research* unexpected recognition, especially among North American stream ecologists. It is the most-cited paper published in the journal according to the Web of Science in December 2006.



Figure 8. From left to right, Russell Death, Kevin Collier and Anne Graesser at The Forks "laboratory", South Westland, in 1986.

Jim introduced me to the North American Benthological Society (NABS) whose meeting in Corvallis, Oregon we attended in 1985. Alan Hildrew (University of London) was the only other non-North American present and the three of us were introduced to the assembled delegates during the opening session. Jim also brought the Pfankuch stability index⁶⁵ to New Zealand and used it in his research. Subsequently, it has been employed successfully by numerous (mainly Canterbury) graduates and I believe we were the first people to use its “bottom component” as a measure of stability relevant to the benthic invertebrate fauna⁹⁸. Unfortunately, for stream ecology Jim chose not to continue with a career in science and is now a highly successful businessman working out of Hong Kong.

Kevin Collier (Figure 8), David

Valentine⁸¹ and Nikolai Friberg, a visitor from Denmark³⁵, carried out further forestry-related stream research and their field studies in Canterbury and Westland greatly increased understanding of the effects of forest type, forestry practices, locality, and water chemistry on forest stream communities. Kevin Collier’s research can also be seen as the point where our interest in forest stream ecology intersected with a growing interest in acidification and low pH.

Acid stream research

My interest in acid streams was stimulated by Alan Hildrew (Figure 9), with whom I spent a period of study leave in 1983. His research with Colin Townsend and numerous graduate students on the streams of the Ashdown Forest in southern England is one of the most comprehensive studies of low-pH streams undertaken and



Figure 9. Alan Hildrew with Annabel Groom and Alan Box in the Ashdown Forest 1983.

has led to an unrivalled depth of understanding of benthic stream communities. The food-web for Broadstone Stream, not far from Poohsticks Bridge, is the most detailed yet published for a stream¹⁰⁹. On my return to New Zealand I realised we had low-pH streams too: the brown water streams draining pakihi in Westland.

Three of my students, Ann Graesser³⁶ (Figure 8), Kevin Collier and Malcolm Main⁶⁰ investigated various aspects of the distribution and ecology of algae, invertebrates and fish, leaf breakdown and water chemistry in these streams. Kevin's wide-ranging research on invertebrate life histories, community composition in relation to pH and aluminium concentration, leaf decomposition, and the construction of a DOC budget for a highly acid stream represents the most intensive study of the "lignin-stained" streams of the Coast¹⁶. The paper he wrote with other members of the Canterbury group in 1990¹⁷ outlines some of the more significant insights we obtained on brown water streams and discussed how streams acidified by organic acids differed from those contaminated by acid inputs of anthropogenic origin. Jennifer Tank's careful work on wood decomposition in West Coast streams of low- and circum-neutral pH showed that microbial biomass and activity were not necessarily lower in brown water streams, and that low nutrient concentrations were likely to have minimised differences in microbial production among her study streams⁷⁷.

Given the history and prevalence of coal mining on the West Coast it is not surprising that streams contaminated by varying degrees of acid mine drainage are also common. Our research on these systems was facilitated by Paddy Ryan

then at the West Coast Regional Council and focused especially on the streams of the Stockton-Denniston Plateau north of Westport. Extensive surveys were undertaken to document water chemistry and invertebrate communities, which not surprisingly are impoverished and dominated by a few species of Chironomidae and stoneflies¹⁰⁵. Melissa Anthony's research in the vicinity of Reefton provided quantitative seasonal data on invertebrate communities under a range of mine-impacted conditions and showed that a hyporheic fauna of insects and crustaceans was present in some of the streams². I also examined aluminium and iron burdens of aquatic plants and animals at different trophic levels with Dr Wayne McDiffett, a North American stream ecologist with broad experience of acid waters in Pennsylvania, but found no evidence for biomagnification of either metal in stream food-webs¹⁰⁶. Unexpectedly, our West Coast research showed that several insect species tolerant of very low pH (<4.5) inhabit streams affected by acid mine drainage in addition to brown water streams, and therefore must tolerate high concentrations of potentially toxic heavy metals such as aluminium.

Individual species, population and community studies

In addition to research that fits neatly into the groupings discussed above, research on streams and aquatic fauna at Canterbury has encompassed less easily classified studies. Much of it has involved the investigation of invertebrate life histories, stream communities, and the effects of disturbance, nutrient limitation, dispersal and colonisation pathways on stream faunas (and to a lesser extent algae). Much of the pleasure obtained from doing

these studies has been provided by the opportunity to use and develop a variety of approaches and techniques, often in combination. For example, we have employed SEM, TEM, GIS, leaf bags, nutrient-diffusing substrata, stable isotope analyses, ^{14}C , enzyme assays, artificial stream channels in the field and in the lab, sticky traps, Malaise traps, freeze-coring and a variety of artificial substrata in addition to conventional sampling, standard light microscopy, chemical analyses and a range of statistical approaches.

Three of my PhD students wrote substantial theses that focussed primarily on aspects of the behaviour and ecology of single species. Trevor Crosby's work on the blackfly *Austrosimulium tillyardianum* has already been mentioned and one of the others was Richard Rowe's study of the damselfly *Xanthocnemis zealandica*⁶⁸. Richard (Figure 10) revised the genus *Xanthocnemis*, described a new species *X. sinclairi*, and made detailed

observations on the behavioural repertoire of the larvae, especially interactions with conspecifics and their use of defended territorial sites. He also investigated the predatory behaviour of *Hemianax papuensis* and demonstrated, unequivocally the occurrence of predatory versatility in odonate larvae. His book "The Dragonflies of New Zealand"⁶⁹ was also written at this time and is a wonderfully detailed, scholarly and valuable contribution to our natural history literature. The third study was Mark Sanders' investigation into the effects of fluctuating lake levels and habitat enhancement on the endangered black stilt *Himantopus novaezelandiae*⁷¹. Mark (Figure 5) made detailed observations on the feeding ecology of stilts on lake shores and river deltas in the Waitaki Basin, and manipulated pond substrata in novel ways to encourage the population growth of those invertebrate species most favoured as food by stilts⁷².

Other highlights were Alan Carpenter's



Figure 10. Richard Rowe with Mike Winterbourn at Cass spring, 1986.

demonstration of protandry in the atyid shrimp *Paratya curvirostris*, which starts adult life as a male and then becomes female¹¹, and Lindsay Chadderton's detailed field study of Stewart Island streams¹². His findings on the distributions of native fish (banded kokopu, giant kokopu and koaro) in the absence of introduced trout provided insights into their likely habitat use on the mainland in earlier times. Furthermore, his observations on the distribution of the isopod *Austridotea lacustris*¹³ and its role in leaf decomposition in Stewart Island streams made significant contributions to understanding one of the largest yet most poorly known stream invertebrates in the country. Lindsay's contemporary, Jon Harding tested the Serial Discontinuity Concept in another extensive field study of West Coast streams and found that contrary to theory lakes and impoundments had little effect on the longitudinal distributions of stream fauna³⁹. Subsequently, he developed a classification of South Island ecoregions based on the faunas of headwater streams and showed that faunal differences among regions were products of land use in addition to geographical factors, climate and water chemistry^{38,41}. Jon has the strong sense of curiosity found in the best naturalists and has made astute field observations of aquatic insect behaviour in the field.

Alastair Suren (Figure 5), who had studied under Sam Lake in Australia was another who made a large contribution to understanding a poorly studied aspect of New Zealand's running waters. His investigations of bryophyte communities in mountain streams demonstrated their significance as habitat for a highly abundant meiofauna⁷⁵, and he showed

that mosses and liverworts provide substrata for algae and trap fine detritus, materials that are primary foods of invertebrates⁷⁶. Algal production in Canterbury and West Coast streams can be light- or nutrient-limited⁹⁷ and Adele Fegley, a visiting student from North America, found that grazing by *Potamopyrgus antipodarum* could have a large effect on epilithic algal biomass and community composition¹⁰³. Mark Ledger, a post-doctoral fellow from Alan Hildrew's group in London, also addressed the question of invertebrate food and found surprisingly, that the larvae of several common stream insects grew efficiently on both algal and detrital diets⁴⁵. He also explored the novel idea that feeding mode was associated with mobility and found that shredders were more mobile than most grazers perhaps reflecting their need to search for a more patchily distributed food resource⁴⁴. Anna McLeod (now Crowe) showed that drift was the main dispersal pathway of mobile insect larvae in Middle Bush Stream at Cass⁵⁹ and a sticky trapping programme undertaken concurrently¹⁰¹, indicated that the adults of *Zelandopsycha ingens* and some other caddisflies with forest-dwelling larvae flew predominantly upstream in conformity with the predictions of Müller's colonization cycle.

Lastly, Gary Scrimgeour and Russell Death (Figure 8) obtained significant insights into the role of disturbance in structuring stream communities. In a study of 10 streams and a wind-swept stony lake shore near Cass, Russell found that species richness and diversity of invertebrates were negatively correlated with disturbance as indicated by a multivariate disturbance index and the Pfanck stability score³⁰. Furthermore, communities at all unstable sites were very

similar and shared taxa that were well adapted for survival and recolonisation following disturbance events. In contrast, communities at stable sites differed markedly, their structure seeming to depend on characteristics of the individual site and possibly biotic interactions²⁹. Some of his more recent work has begun to tease out the relative importance of disturbance *per se* and primary production on benthic community structure³¹. Russell was the most mathematical of my students and the most interested in testing competing theories of community structure.

Gary Scrimgeour monitored the recovery of the *Deleatidium*-dominated benthic fauna of the Ashley River following a major flood and the speed of recovery suggested that insect larvae of various sizes were able to recolonize from

local refugia⁷³. These are likely to include minor braids and spring-fed seeps, which Bruce Digby showed were more productive than the main channels of braided rivers³². Sue Adkins' finding of a diverse community of aquatic insects down to at least 30 cm in two small streams at Cass¹, supports the notion that refuges from floods may also occur within the streambed. Larvae of one of these insect species, the common cased caddis *Olinga feredayi* feed on hyporheic biofilms and buried fragments of detritus, although an experiment carried out by Mark Ledger and Greg Burrell (Figure 11) indicated that hyporheic biofilm alone was insufficient to support larval growth¹⁰. It seems likely that *Olinga* larvae migrate vertically within the streambed in search of high quality patches of detritus and algal-based biofilm.



Figure 11. Greg Burrell with 4th year Limnology students at the Lake Sarah *Uropetala* site, 1999. Angus McIntosh is on the right.

Notable advances in NZ stream ecology since 1970

Freshwater biology has advanced on many fronts in New Zealand in the last 30 years or so as it has in much of the western world. Many more graduates have been produced and the opportunities for employment have increased dramatically. In 1970 most of our few stream biologists worked at universities or in fisheries research, whereas now they are also represented in large numbers at NIWA, on regional councils and as consultants. Much interesting freshwater research has been done during this time, one of the first large-scale projects being the insightful study of the Rotorua lakes by the newly established DSIR freshwater group⁵². It warned of the threat to the lake ecosystems of intensifying land use in their catchments, but like earlier studies on the Rotorua lakes and Waikato River impoundments¹⁵ little heed was taken of its message and today the quality of the Rotorua lakes continue to decline. More recently, the 100-rivers project resulted in the collection of much fundamental data on the chemistry, hydrology and biology of rivers throughout New Zealand⁵ and has provided a baseline against which future comparisons can be made. The following four projects and programmes also stand out in my mind.

Development of the MCI

The Macroinvertebrate Community Index (MCI) was developed by John Stark based on collections made in streams and rivers of the Taranaki Ring Plain⁷⁴. It was the first biology-based index developed in New Zealand to assess the water quality / health of streams and now includes quantitative and semi-quantitative versions in addition to the original one

that is based on presence-absence data. The MCI has become the standard monitoring tool used by regional council biologists to monitor the state of their streams and is used widely to investigate the effect of organic pollution on running waters. Because it is simple to calculate and easy to evaluate the MCI can be used by persons with only limited knowledge of freshwater biology. At present it has no serious challenger as a stream monitoring tool in this country.

The University of Otago stream research programme

The stream research group at Otago led by Colin Townsend has provided significant insights into the roles of biotic interactions within stream communities and their influence on assemblage structure. Their studies have demonstrated that New Zealand stream communities are not solely dominated by physical factors such as flow variation and disturbance, and that predation, competition and other biological interactions can have significant effects. Notable examples are the study by Townsend and Crowl⁸⁰ that showed that trout had a major effect on the distribution of galaxiid fishes in the Taieri River, and the work of McIntosh who demonstrated that fish odours influenced the foraging and drift activity of mayfly nymphs with consequences for their growth and fitness⁵³. The group has also reported the occurrence of trophic cascades in foodwebs involving algae, invertebrates and fish⁶, and shown that predators can affect foodweb architecture in stable New Zealand streams.

Stream algal research at NIWA

The sustained research of Barry Biggs and collaborators has made a major

contribution to our knowledge of algal communities in streams and rivers and the factors that regulate the distribution and abundance of algae. Barry has characterised periphyton communities in many kinds of rivers of different trophic states and his largely field-based research has shown that flood disturbance frequency, nutrient supply and insect grazing have the strongest effects on algal accrual and loss in New Zealand rivers⁷. Furthermore, his work on nutrient-biomass relationships has led to the formulation of guidelines to prevent algal proliferations and more generally to maintain in-stream values. His research group has also produced authoritative manuals for the identification and monitoring of periphyton taxa^{4,8}. Barry has justifiably obtained a strong international reputation and has raised the profile of New Zealand limnology through the quality of his research.

Maintenance of sex in Potamopyrgus antipodarum

I described most of the larval trematode parasites that use *P. antipodarum* as an intermediate host⁹³, including the abundant *Microphallus*, which has a central role in Curt Lively's outstanding research on the maintenance of sex by the snail. Hence, his research findings have been a constant source of interest to me. Since the mid-1980s when he came to the Zoology Department at Canterbury as a post-doctoral fellow, Curt along with some of his colleagues and students have spent most summers in New Zealand studying aspects of the snail's evolutionary biology. Populations of this remarkable species include asexual clones and sexually reproducing individuals whose continuing occurrence appears to be maintained by parasitism⁵⁰. Larval trematodes also affect

the behaviour of snails making transmission of the parasite to a definitive host more likely⁴⁶. Furthermore, clonal snails may be adapted to particular habitats within a lake and a remarkable 165 clones were identified from 605 snails collected from Lake Alexandrina³⁴. Some of the group's more recent research has been addressing the question of the age of clones and their distribution and dispersal within New Zealand in evolutionary time⁶³. Curt Lively's research is of the highest intellectual quality and has been recognised by his election to the fellowship of the American Academy of Arts and Sciences.

Concluding remarks

The 1970s to 90s were a golden age for stream ecology. A major reason for that was the recognition that streams are an integral part of their catchments⁴³ and that catchment geology, vegetation cover and land use all play significant roles in determining the nature of stream communities and regulating stream ecosystem function. The development of stream theory, most notably the River Continuum Concept⁸², stimulated a large body of research on running water throughout the world, much of which was drawn together in 1995 in a comprehensive volume with an international perspective²⁷. The introduction of functional feeding groups, application of the Intermediate Disturbance Concept to streams, and the development of the Flood-Pulse and the Serial Discontinuity Concepts among others, presented the opportunity for stream ecologists to test ideas and obtain a more focused view of "how streams work". Furthermore, concurrent increases and improvements in technology enabled

more sophisticated and precise studies to be undertaken. Despite the many advances evident in our knowledge of stream ecology, many challenges remain. Important ones relate to the application of research-based knowledge to sustain ecological values of streams and rivers in the face of catchment development, increasing demands for water, threats from invasive species and long-term climate change.

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